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# Dichotomy of eutherian reproduction and metabolism

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**Abstract**

How anatomical, physiological and ecological (life history) features scale with body mass is a fundamental question in biology. There is an ongoing debate in the scientific literature whether allometric scaling follows a universal pattern that can be described in a single model, or differs between groups. However, recently some analyses were published demonstrating a change in scaling across the body mass range: brain-size allometry of mammals indicates that scaling follows a curvilinear pattern in double-logarithmic space, and a quadratic pattern in double-logarithmic space was found in one of the largest physiological datasets, on basal metabolic rate (MR) in mammals. Here, we analysed a variety of independent datasets on anatomical, physiological and ecological characteristics in mammals, birds and reptiles to answer the question whether the quadratic scaling is a universal biological law, or a pattern unique to mammals. The pattern was present in mammalian basal and field MR, brain size, and reproduction parameters, but neither in other organ allometries in mammals, nor in the scaling of MR in birds and reptiles. However, the curvature was better explained by separate allometric scaling of three different mammalian reproduction strategies: marsupials, and eutherian mammals with one and with many offspring. The two latter strategies are distributed unequally over the body mass range in eutherian mammals. Our findings show that a quadratic model, as well as a traditional allometric model with a universal scaling exponent (such as 0.67 or 0.75), may be inappropriate in mammals as they are a result of different scalings within these three reproductive groups. We propose that the observed distribution pattern is the result of the eutherian mammal clade's uniquely pronounced dichotomy of reproductive strategies.

**Keywords:** basal metabolic rate, field metabolic rate, life history, metabolic theory of ecology, brain size, expensive tissue hypothesis

The traditional concept has metabolism (metabolic rate, MR) scale allometrically to body mass (M) as a power function

$$MR = a\, M^{b}. \quad (1)$$

This equation becomes linear when log-transformed

$$\log(MR) = \log(a) + b \log(M). \quad (2)$$

In the framework of a 'metabolic theory of ecology', other life history traits are linked to the allometry of MR (Lovegrove 2000, Dodds et al. 2001, Brown et al. 2004, Glazier 2005, White and Seymour 2005). Predictions of equation (1) have therefore been used extensively to describe scaling relationships in biology and ecology. The allometric scaling exponent *b* is usually between 0.67 and 0.75 in mammals, and its biological meaning is at the core of a long-standing debate.

An expanding view is that *b* is not constant but varies depending on the M range of the dataset (Lovegrove 2000, Dodds et al. 2001, Glazier 2005, White and Seymour 2005) or on the taxonomic composition of the sample (Hayssen and Lacy 1985, Sieg et al. 2009, White et al. 2009, Capellini et al. 2010). Recently, several research groups have suggested that mammal basal MR (BMR) is non-linearly linked to M in log-log plots (double-logarithmic space), and can be better described by a quadratic function (Clarke et al. 2010, Isaac and Carbone 2010, Kolokotrones et al. 2010); actually, a better fit of a quadratic function had already been described by Hayssen and Lacy (1985) but had received little attention. Curvature arises because the allometric exponent *b* varies as a function of M on a logarithmic scale, thus

$$b\,(M) = b_1 + b_2 \log(M). \quad (3)$$

Substituting *b* (M) for *b* in equation (1)

$$MR = a\,(M)^{(b_1 + b_2(\log(M))}, \quad (4)$$

and log-transformation gives the quadratic function

$$\log\,(MR) = \log(a) + b_1 \log(M) + b_2\,(\log(M))^2. \quad (5)$$

67 Equation (4) reflects that the exponent term changes systematically with M
68 (Kolokotrones et al. 2010). In this approach the magnitude of the parameter estimates for $a$
69 and $b_1$ (but not $b_2$) depend on the unit of M; however, the full exponent term [$b_1 + b_2 \log(M)$]
70 is constant for a given M independent of the unit of M, and increases in a consistent manner
71 with M (Fig. 1b in Kolokotrones et al. 2010).
72 In relaxing the assumption of a fixed allometric exponent, quadratic approaches to
73 metabolic scaling have the potential to unravel new trends in the evolution of life history
74 traits. A convenient interpretation of the quadratic scaling pattern is that, as mammals become
75 smaller or larger than some hypothetical M mid-point, they both increase their MR beyond
76 the general simple power allometry. Bats – which we will use repeatedly as an example here –
77 appear to be one exception (of several) to that pattern, with lower BMR than many mammals
78 of similar M (Fig. 1a).
79 However, the finding of such a quadratic scaling in mammalian BMR (Kolokotrones
80 et al. 2010), but apparently not in birds, reptiles or fish (Isaac and Carbone 2010), raises the
81 question whether quadratic scaling is (1) a universal principle, and (2) whether it is a
82 physiologically relevant characteristic of mammals or an empirical yet ambiguous
83 characteristic of the mammal MR dataset. The recent finding of a similar nonlinear scaling of
84 mammalian brain mass in logarithmic space (though with an opposite curvature; Albrecht et
85 al. 2010) supports the notion that quadratic scaling might be a universal characteristic at least
86 within mammals. Here, we explore various datasets on anatomical, physiological and
87 ecological characteristics of organisms for their scaling patterns, demonstrate quadratic
88 scaling in a variety of mammalian datasets, and offer an explanation why this scaling pattern
89 probably does not represent a universal law but is an artefact typical for certain mammal
90 datasets, because it reflects different reproductive strategies that are represented by species of
91 different body mass ranges.
92

93 **Methods**

94 We analysed datasets (see Table 1 for sources) for BMR in mammals, birds and reptiles, as
95 well as datasets for field MR (FMR) for these three clades, and independent datasets on
96 mammal characteristics that are functionally linked with MR. We analysed datasets on
97 mammal organ masses (brain, heart, liver, kidney, lung, digestive tract), breathing frequency,
98 alveolar lung surface area, heart rate, produced offspring mass per year and female, and the
99 maximum population growth rate ($r_{max}$). However, a major limitation of several of these
100 mammalian datasets is that the sample size is distinctively lower than that of the BMR dataset
101 (see Table 1), and that overlap of species covered between the datasets is limited.

102 All mass data, including body mass (M), were transformed to a kg-basis. Metabolic
103 rates were expressed as kJ $d^{-1}$. Log-transformed data were first subjected to least-squares
104 regression analysis considering a linear function (equation 2) and a quadratic function
105 (equation 5) using the Non-linear Estimation procedures of STATISTICA V8.0 (Gauss-
106 Newton method, 1000 iterations) (Statsoft_Inc 2007). When the fitting procedure converged
107 on significant parameter estimates for functions (95% confidence limits for $b$, or $b_1$ and $b_2$
108 exclude zero), we compared goodness-of-fit using the small-sample Akaikes Information
109 Criterion ($AIC_c$) (Burnham and Anderson 2002). We calculated the $\Delta AIC_c$ for each model
110 ($AIC_c - \min(AIC_c)$), and followed the evaluation process suggested by Burnham and
111 Anderson (2002): $\Delta AIC_c$ scores less than 2 imply well-supported models, scores between 2
112 and 10 imply moderate support, and a score > 10 indicates a weakly-supported model relative
113 to the alternative. Note that, as stated in the discussion, we do not hypothesize that the
114 curvature is a real biologically meaningful effect, but an artefact produced by a dichotomy in
115 reproductive strategies across the body size range in eutherian mammals.

116 To test our prediction, we used only those datasets in which quadratic scaling yielded
117 a better fit than the linear scaling in mammals. We divided the eutherians into two groups:
118 species with ≤ 1.5 offspring per year (single offspring) and those with > 1.5 offspring per year

(multiple offspring), based on information on the number of offspring (per year) from the dataset on reproductive characteristics. This classification was used to avoid discussions about differences between altricial and precocial status of offspring, and to remain consistent within the dataset without adding information from other sources. The general linear and quadratic regressions of the log-transformed data were additionally compared (again using $AIC_c$) to models of separate, or composite, linear regressions for marsupials/monotremes and eutherians, and for marsupials/monotremes and eutherian species with $\leq 1.5$ and $> 1.5$ offspring per year.

In order to control for the effect of common ancestors, the two-step analyses of mammal datasets were repeated using the Phylogenetic Generalized Least-Squares (PGLS) approach (Pagel 1999, Freckleton et al. 2002) in which a well-developed standard statistical method was extended to enable the inclusion of interdependencies among species due to a shared evolutionary history. Phylogenetic relationships among species were inferred from the mammal tree given by Bininda-Emonds et al. (2007). They were adapted to each dataset by removal of species not included in the respective dataset from the overall mammal tree. PGLS analyses for linear and quadratic models were conducted using Pagel's "lambda" Correlation Structure (corPagel) in R (version 2.11.2) applying the packages ape (phylogeny) and nlme (fitting of linear and non-linear models using generalized least squares; functions gls and gnls). Since to our knowledge PGLS analysis cannot be conducted for composite regression models, goodness-of-fit of models via AIC values could not be assessed to the same extent for the PGLS analyses. However, in order to asses whether PGLS analyses supported a difference in slopes between our different reproductive groups, we also analysed a linear model with an intercept term for the reproductive groups and an interaction term (reproductive groups and body mass) (Kabat et al. 2008).

Datasets for mammal and bird BMR are sufficiently large for further interrogation, to test the robusticity of the statistical analyses. In particular, we explored the sensitivity of each

test on the size of a sample and the distribution of M within it (see supplement). For example, if the quadratic regressions are an artefact of some datasets, then the significance of the parameters (especially $b_2$) and goodness-of-fit relative to linear regressions would decline with a (1) smaller sample, (2) a smaller range of M or (3) a M distribution that does not extend above or below a threshold required for detection of such curvature. Also, derivation of the quadratic function requires that the allometric scaling exponent ($b$) is linearly related to M on a logarithmic scale, a condition we explicitly test for in these procedures. These explorations should indicate the likelihood of (1) detecting spurious quadratic fits, and (2) detecting instances where M distributions are insufficient for a significant polynomial fit, e.g. in smaller datasets. We used randomized resampling of subsets of data to explore this sensitivity in both regression functions. From the two datasets, random subsamples of 10 %, 25 %, 50 %, and 75 % of the data were extracted, the significance of their parameters checked, and goodness-of-fits compared. For each subset we performed $3 \times 10^4$ permutations. Significance ($p$-value) was calculated as the number of occurrences of a satisfied condition (e.g. parameter confidence intervals exclude 0, significance of regression, lowest $AIC_c$ score) divided by the number of permutations. Randomization was carried out using the PopTools v3.0.6 Add-in package for MS-Excel (Hood 2008).

**Results**

We found that a quadratic scaling provides a better fit to empirical data on BMR and FMR in mammals (Fig. 1a,c; Tables 3 and 4), but not in reptiles (Fig. 1b,d; Table 2). When testing the sensitivity of each test on the size of a sample and the distribution of M for mammalian basal MR, we found that the significance of the polynomial term of the quadratic regression is only evident when the M range is at least 4, possibly 5, orders of magnitude, and support for a quadratic over a linear fit is reduced in smaller datasets, for example if the data do not include species below 0.01 kg or above 1000 kg (results shown in Supplement). For birds, quadratic

171 scaling was not evident in the FMR dataset (Fig. 1d). For BMR, the quadratic scaling yielded
172 a significant regression for the entire avian dataset (Fig. 1b; Table 2); this effect was lost,
173 however, when smaller subsets were used for the analysis (see Supplement), indicating again
174 random significance of a quadratic fit.
175 For most mammalian anatomical and physiological datasets, no significant quadratic
176 scaling was found (see Supplement, Table S2). In contrast, brain size showed a negative
177 quadratic scaling (Fig. 2, Table 5), offspring mass showed a positive quadratic scaling (Fig. 3,
178 Table 6), and population growth rate ($r_{max}$) again showed a negative quadratic scaling (Fig. 4,
179 Table 7). After controlling for phylogeny, the observed quadratic scaling was still significant
180 in BMR, FMR and brain mass, but not in offspring mass and $r_{max}$ (Tables 3-7).
181 When various approaches to explain the quadratic scaling by differences in simple
182 scaling patterns between the three reproductive mammal groups were tested with composite
183 linear regressions, solutions that considered marsupials and eutherians, and marsupials and
184 eutherians with single and multiple offspring separately, were always among the best-
185 supported models (Tables 3-7). The difference in $AIC_c$ scores for quadratic compared with
186 best-supported composite linear models (i.e. $\Delta AIC_c$) ranged from 11 to 833; for the field MR
187 data – the smallest dataset amongst those subjected to these tests – this difference barely
188 exceeded 2. Using PGLS, a composite approach cannot be assessed; however, a linear
189 approach with an interaction term for the reproductive groups was as supported as the
190 quadratic approach ($\Delta AIC_c < 2$) for BMR (Table 3), and was the best-supported model for
191 brain mass, offspring mass, and $r_{max}$ (Tables 5-7). With PGLS, the quadratic approach was the
192 best-supported model without alternative only for FMR (Table 4).
193 For BMR the analysis of raw data yielded significant differences in the scaling
194 exponent between the two eutherian groups (none of which differed significantly from the
195 marsupials). Eutherians with single offspring had a steeper allometric scaling at $M^{0.76\ (95\%CI}$
196 $^{0.74,\ 0.78)}$ than eutherians with multiple offspring at $M^{0.69\ (0.67,\ 0.71)}$(Table 3). The scaling of

offspring mass differed in the same direction, with $M^{0.80\ (0.77,\ 0.83)}$ in eutherians with single offspring and $M^{0.67\ (0.62,\ 0.71)}$ in eutherians with multiple offspring (Table 6). Correspondingly, the negative scaling of $r_{max}$ was steeper in eutherians with multiple offspring at $M^{-0.29\ (-0.35,\ -0.23)}$ than in eutherians with single offspring at $M^{-0.12\ (-0.16,\ -0.09)}$ (Table 7). The scaling exponent of brain mass did not differ significantly between the eutherian groups (overlapping 95% CI from $M^{0.69}$ to $M^{0.72}$); however, the intercept (*a*) differed significantly between the groups, with a higher level in eutherians with single offspring (Table 4) than in eutherians with multiple offspring.

## Discussion

The results indicate that some scaling occurs in mammals that can be described by the quadratic model; depending on the dataset, this quadratic scaling is or is not significant after correcting for the influence of phylogeny. The presence of quadratic scaling in both BMR and FMR data supports the interpretation that this pattern is a true characteristic of mammals and not a spurious finding of a particular dataset. However its absence in reptiles and birds (found by Isaac and Carbone 2010 and corroborated by different datasets in this study) suggests that this scaling pattern may not necessarily be universal. This, and the fact that quadratic scaling was not evident in smaller subsets of the BMR data as detailed in the Supplement, indicates that this scaling pattern might not be linked to a universal theory of resource distribution networks (Savage et al. 2008, Kolokotrones et al. 2010). The repeated finding of quadratic scaling indicates that fitting other than simple allometric equations to empirical data might be a promising approach in comparative physiology. However, rather than just searching for an equation with a higher fit, the choice of equations needs to be based on a theoretical background. Because quadratic scaling does not appear to be universally supported in the various datasets, being rejected either after controlling for phylogeny or when testing various subsets of the data (see Supplement), assuming an effect of different scaling exponents (or

intercepts) for different functional groups is the most parsimonious approach. It appears that quadratic scaling in these datasets – if it is detected – arises as an artefact of two different simple scaling mechanisms that exist in varying predominance at different ranges of the M spectrum of eutherians. Note that this is not only an effect of simply splitting the mammal body size range in two distinct subunits: while the body mass range of eutherians with more than one offspring is actually limited insofar as very large forms are excluded, the group of eutherians with a single offspring comprises the full mammalian body size range (Fig. 1-4, where bats are among those species included in the regression of eutherians with a single offspring). This dichotomy may help explain why, when analysing mammal BMR data in body size bins, there is little variation in the largest size classes but considerable variation in the lower ones (Clarke et al. 2010) – where the two different reproductive modes coexist. For these reasons, quadratic scaling should in our view be considered only as a tool for detecting multiplicity in allometric exponents (or intercepts), but not necessarily for explaining overall allometric relationships.

Morphological data (organ masses) and other physiological measurements did not indicate a quadratic scaling. This could be attributed to their low sample size, but it should be noted that low sample size did not prevent the general detection of a quadratic pattern in the mammal field MR dataset. The only exception among the morphological measurements was brain mass. The finding that brain mass shows a quadratic scaling pattern of opposite curvature, i.e. with both very small and very large animals having lower brain masses than predicted by a simple allometric regression, corroborates a recent identical finding by Albrecht et al. (2010). The opposite direction of the curvature, and the difference in the scaling pattern compared to that of the BMR or the offspring mass (with a difference in the intercept *a* but not in the scaling exponent *b*), suggest that this general shape of brain mass scaling cannot be explained by a direct link between brain mass and BMR. Actually, a variety of strategies of both, the individual carrying a large brain or the mother producing the

offspring with a large brain, are currently considered important correlates of adult brain size, with the level of BMR being just one among several parameters (Isler and van Schaik 2009, Martin and Isler in press). Generally, there is a trade-off between the intensity of MR and the time during which energy is invested in development (of brain tissue, for example) (Isler and van Schaik 2009, Weisbecker and Goswami 2010, Martin and Isler in press).

The metabolic theory of ecology predicts a fundamental influence of MR on ecological differences between species (Brown et al. 2004). Quadratic allometric scaling might therefore be more evident in ecological than morphological parameters. In mammals, reproductive strategies are closely linked to life history, for which large comparative datasets are available (Duncan et al. 2007, Jones et al. 2009). The annual offspring mass per female and the maximum population growth rate (a proxy for the number of surviving offspring) are also better explained by a quadratic than by a simple power function in the raw data (Figs 3a and 3b, Table 6 and 7). This means that for their respective M, very small and very large mammals produce more offspring mass and more surviving offspring per unit time than expected based on a simple allometric relationship (note that bats are again an exception, with lower offspring mass than similar-sized small mammals - a possible adaptation to flight; Hayssen and Kunz 1996). In particular, the similarity of the scaling exponents between BMR and offspring mass in eutherians, and the reciprocal ranking of the BMR and the $r_{max}$ scaling exponents, support some kind of functional link between BMR and these life history parameters. On the other hand, the fact that curvature in the BMR dataset remained significant when considering the evolutionary history of species, but not in the offspring mass or $r_{max}$ datasets, could indicate that the two groups of characteristics are not as closely functionally linked as proposed by metabolic theory. Alternatively, this could be the effect of differences in the taxonomic composition of the datasets used, alone or in combination with the response effect (e.g. offspring mass shows a dramatic dichotomy between eutherians and marsupials). Further analyses are required to corroborate the link between BMR and life history.

In four of the five cases where quadratic scaling was detected in the raw data, a combination of linear models taking into consideration the various mammalian reproduction modes – marsupials, and eutherians with few and many offspring - provided a substantially better fit to the data than a quadratic model (and indeed a linear model with universal scaling exponent). Actually, there were different scaling relationships between the two reproductive strategies in eutherians that combine to determine the shape of the overall relationship, but not between each of the eutherian strategy and the marsupials. The difference in the scaling exponent for BMR and offspring mass between single- and multiple-litter eutherians is similar to those described for MR (Lovegrove 2000, Dodds et al. 2001, Glazier 2005, White and Seymour 2005) between large and small mammals. A similar split of $r_{max}$ according to the reproductive strategy (defined as the production of altricial or precocial offspring) was also already described previously (Hennemann 1984); and again, a similar split is evident in data on foetal growth between altricial and precocial mammals (Martin and MacLarnon 1985).

Further studies should aim at investigating scaling patterns for MR and other morphological and physiological measurements not only on the basis of individual taxonomic groups (such as e.g. by White et al. 2009), but on the basis of functional groups. Such an approach allows to formulate hypotheses on the relationship of a functional adaptation and the level of metabolism, and was widely used by McNab (2008, 2009), who concluded that BMR in mammals and birds varied with natural diet, habitat, climate, the use of torpor, or the ability to fly. Kolokotrones et al. (2010) found that even when all these factors were considered, a quadratic scaling pattern still persisted in the mammal basal MR dataset. We propose this is because the reproductive strategy – in terms of the number of offspring produced by eutherians – was not among the factors they analysed. The fact that the reproductive strategy was not included in previous studies must be considered a coincidence that should be addressed in the future.

We conclude that the quadratic scaling inherent in various datasets confirms findings that no common simple allometric scaling should be assumed as universal – neither for MR, life history, nor morphophysiological measurements –, but indicates the existence of relevant sub-groups that need to be investigated separately. We suggest that quadratic scaling in metabolic rates is an artefact of different scaling laws in eutherian mammals with different reproductive strategies, which are correlated to body size: the strategies to produce many small offspring in many small (but no very large) species, or to produce few large offspring in basically all large (and some small, including bats) species (Derrickson 1992). We propose that the unique dichotomy of these strategies along the M gradient gives the eutherian MR and life history curves their typical curvature shapes.

Our distinction of eutherians according to number of offspring somewhat resembles the classification of precocial and altricial offspring. Martin and MacLarnon (1985) already stated that the difference between precocial and altricial mammals was *'a particularly convincing example of major allometric grade distinctions'*. However, there is an important difference between classifying eutherians according to the precocial/altricial dichotomy and the number of offspring produced. Bats represent one exceptional group of small mammals (among several). Bat neonates are usually considered 'altricial'. Bats are, however, possibly due to their adaptation to flight, limited in their number of offspring and might represent, so to speak, allometric extrapolations to the low M range of the BMR, offspring mass and $r_{max}$ patterns typical for large mammals that also only produce one offspring. This finding should be corroborated in more detailed analyses; it could suggest that not only the precocial or altricial state of the offspring itself, but more so its number may be an important physiological characteristic between species.

Why is the strategy of having multiple offspring limited to the lower body size range? Multiple offspring are mostly altricial, with few exceptions (Derrickson 1992); single offspring are often precocial, with more exceptions. Simple reflections not correlated to

energetics could give ultimate explanations for why larger animals do not produce many (altricial) offspring. For example, animals of large body size will have more difficulties in hiding altricial young from potential predators; note that the largest altricial mammals are mostly predators themselves that often use denning (bears) or cooperative breeding (other carnivores). If such extrinsic or ecological factors were responsible for the observed pattern, we would intuitively expect a scenario in which the production of multiple offspring is either

a) simply linked to the same offspring mass (and MR) with more but smaller offspring, with identical slopes of the BMR or offspring mass scaling pattern between eutherians of different litter size (Fig. 5a) or

b) linked to a consistently higher offspring mass (and MR) with parallel slopes of the BMR or offspring mass scaling pattern between eutherians of different litter size (Fig. 5b).

These patterns are both not consistent with the empirical data.

However, the similarity in scaling of MR and reproductive patterns also gives rise to an ecophysiological, proximate explanation based on allometric scaling patterns. Given two groups of animals with different levels of MR, we predict that the group with the higher MR could outcompete the other because of its higher potential reproductive output (chapter 13 in McNab 2002). The low M range, however, may offer animals with a comparatively low MR, that produce less offspring mass, ample ecological niche space (with bats, as flyers, the dramatic example; other blatant examples could be burrowing animals with their typically low metabolism, (McNab 1966)). Thus, in the low M range, both reproductive strategies can occur (Fig. 5c). Actually, the discussion about the differences between altricial and precocial mammals appears to focus on the perceived ‘advantage’ of altricial species, for example in terms of their higher potential for population growth, when compared to precocial mammals *of similar size* (e.g. Hennemann 1984). Less attention has been drawn to the fact that the different allometries of mammals with many and few offspring intersect at a certain M range,

and that above this intersection, mammals with few offspring will be at an advantage in terms of MR, offspring mass, or population growth (Fig. 5c). In the high M range, where the difference in MR between the reproductive strategies is reversed, animals with a single offspring, and a steeper MR scaling, thus predominate. Niche space is less diverse for larger animals, and animals with a reproductive strategy of multiple offspring, with their putatively lower metabolism at high BM, therefore find no niches to support them in this M range (Fig. 5b). Evidently, the intersection should not be treated as a certain M point but as a range in which some altricial mammals may adopt certain strategies, such as for example cooperative breeding with or without breeding suppression (Creel and Creel 1991), to maintain high levels of reproductive output.

These reflections raise the intriguing question why channelling resources to one single offspring should allow a steeper scaling of MR than the production of multiple offspring. Is this difference the effect of one physiological mechanism for all mammals, or a combination of several different mechanisms, and why do these scaling relationships intersect at a certain M range? Are scaling patterns within taxonomic and functional groups really best represented by a linear (simple allometric) approach (regardless of differences in the scaling coefficient), or do various scaling patterns coexist between such groups? Does the similarity in the scaling of BMR and offspring mass reflect a causal relationship, or only the influence of a third mechanism on both physiological measures? Do these scaling relationships differ in a relevant way once body temperature effects are included in the analyses? All these questions clearly warrant more detailed investigation. Whatever the reason for the difference in the scaling patterns – these patterns also stimulate speculation about potential conceptual predominance of large mammals over terrestrial birds and the only (many offspring-producing and potentially endothermic) sauropsid group that reached equally large body sizes – the dinosaurs.

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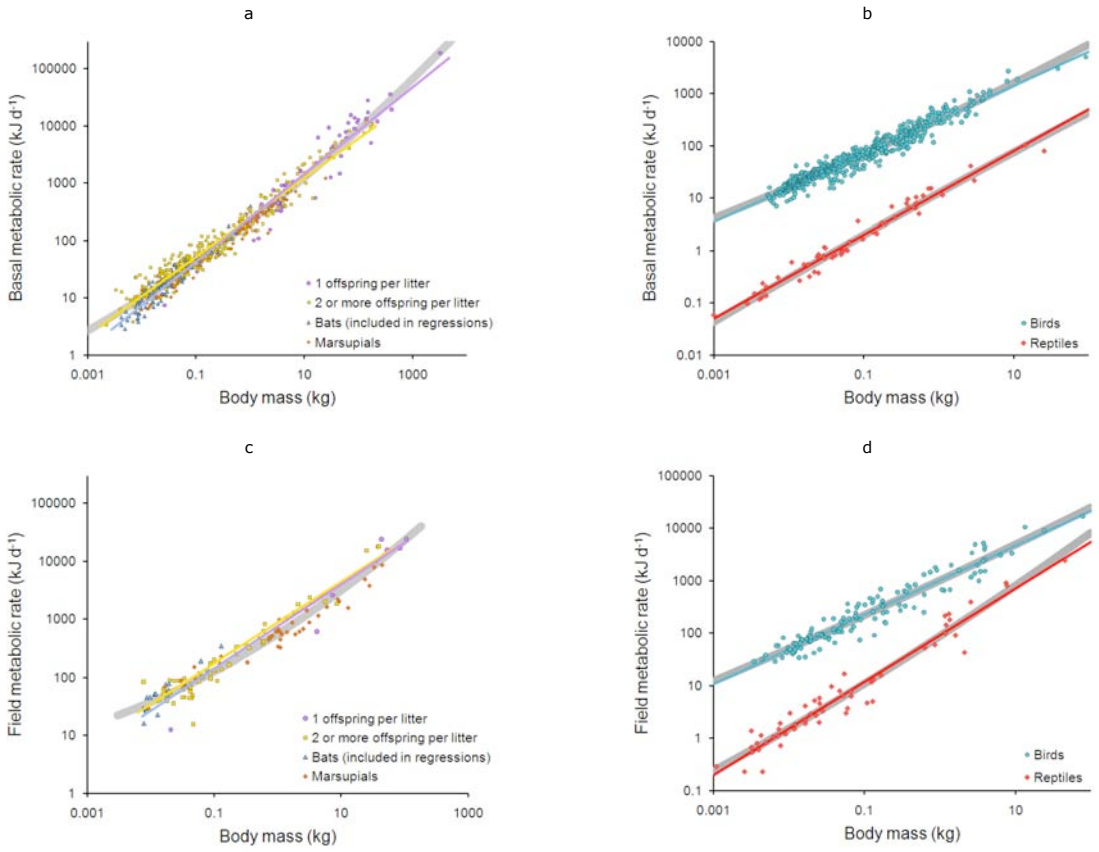


493
494 **Figure 1** Relationship of body mass and basal metabolic rate in mammals of different
495 reproductive strategies (a), birds and reptiles (b), and field metabolic rate in mammals of
496 different reproductive strategies (c) and birds and reptiles (d). Linear regressions of the
497 different reproductive groups (same colour as plots) as well as the curvature model for the
498 whole dataset (grey shadow) are presented. For statistics, see Table 2, 3, and 4. Note that bats
499 are included in the regression for eutherians with one offspring per litter.
500

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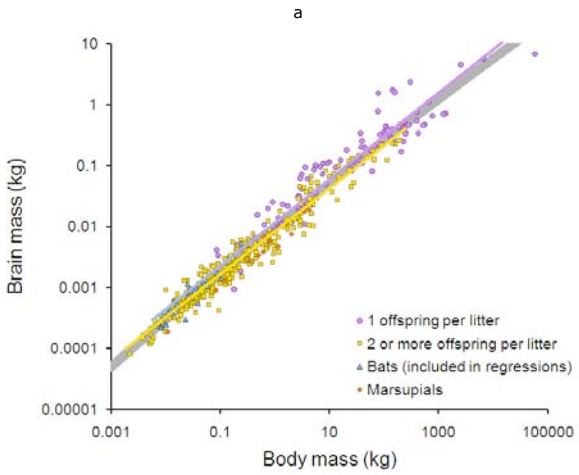
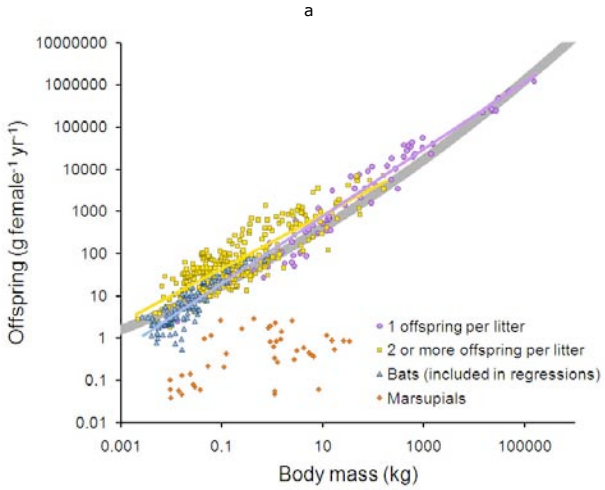



501

502 **Figure 2** Relationship of body mass and brain mass in mammals of different reproductive
503 strategies. Linear regressions of the different reproductive groups (same colour as
504 plots) as well as the curvature model for the whole dataset (grey shadow) are
505 presented. For statistics, see Table 5. Note that bats are included in the regression for
506 eutherians with one offspring per litter.

507

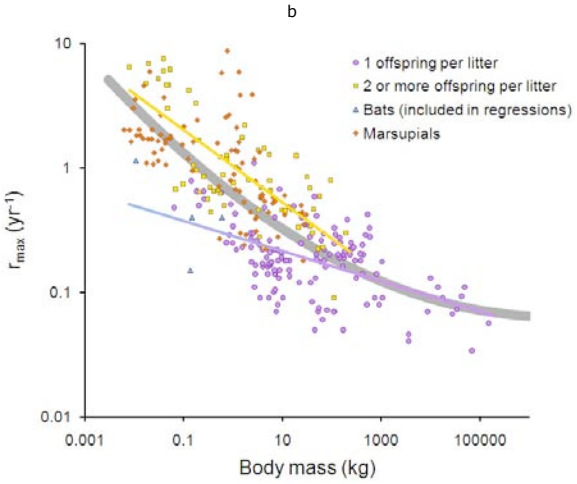



508

509 **Figure 3** Relationship of body mass and mass of offspring per female and year in mammals
510 of different reproductive strategies. Linear regressions of the different reproductive
511 groups (same colour as plots) as well as the curvature model for the whole dataset
512 (grey shadow) are presented. For statistics, see Table 6. Note that bats are included in
513 the regression for eutherians with one offspring per litter.

514

515




516

517 **Figure 4** Relationship of body mass and $r_{max}$ per year in mammals of different reproductive
518 strategies. Linear regressions of the different reproductive groups (same colour as
519 plots) as well as the curvature model for the whole dataset (grey shadow) are
520 presented. For statistics, see Table 7. Note that bats are included in the regression for
521 eutherians with one offspring per litter.

522

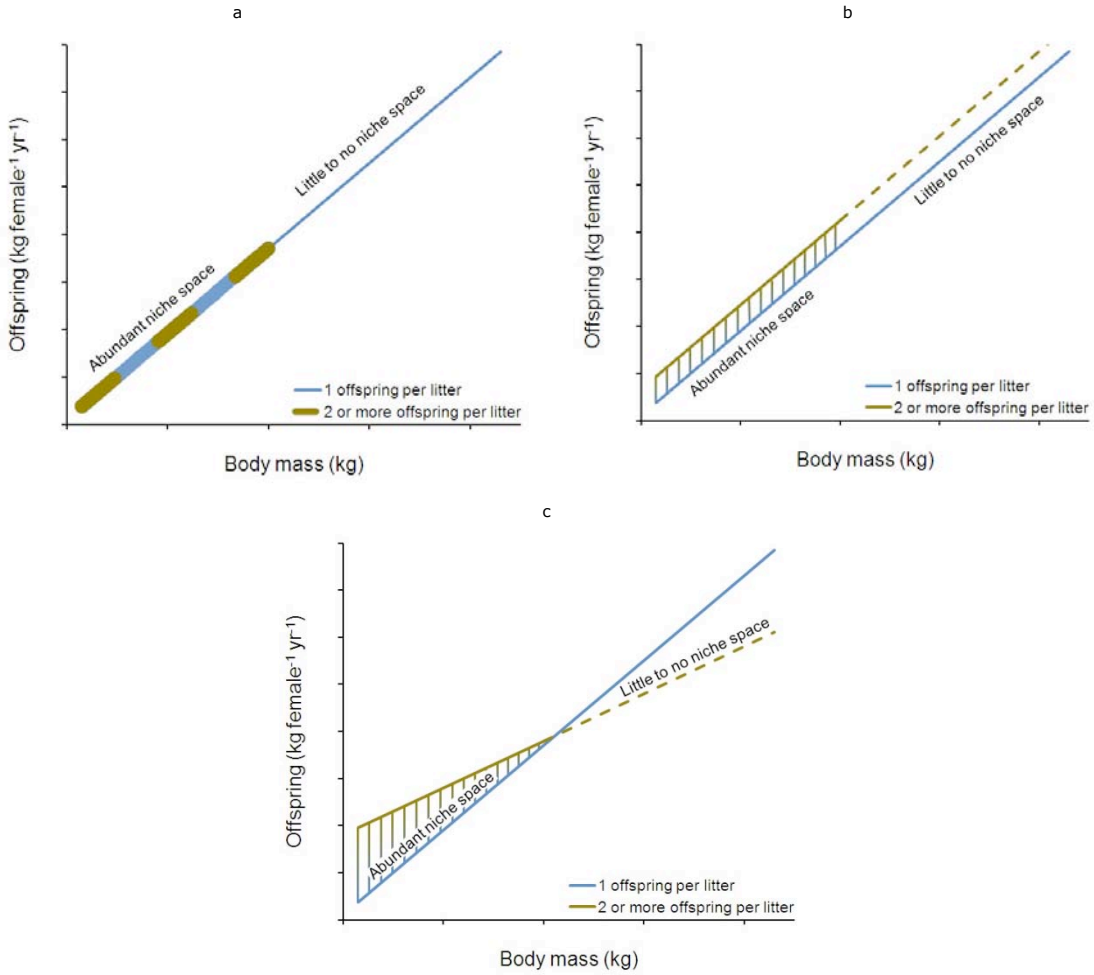



**Figure 5** Hypothetic models (a, b) and a model for the observed situation (c) of the relationship between body mass (M) and mass of offspring per year and female in eutherians of different reproductive strategies. Whereas in the small M range niche space is abundant and thus both reproductive strategies are present, niche space is less diverse for species in the high M range, and animals with a reproductive strategy of multiple offspring, with their putatively lower metabolism at high M, therefore find no niches.

532 Table 1. Datasets used for this study (n=number of species)
533

| Trait | unit | Group | n | notes | Data source |
|---|---|---|---|---|---|
| Basal metabolic rate (BMR) | kJ $d^{-1}$ | Mammals | 615 | | (McNab 2008) |
| | | Birds | 530 | | (McNab 2009) |
| | | Reptiles | 55 | using only data for 20°C at rest | (Andrews and Pough 1985) |
| Field metabolic rate (FMR) | kJ $d^{-1}$ | Mammals | 120 | marine mammal data read from graph | (Speakman and Król 2010) |
| | | Birds | 130 | | |
| | | Reptiles | 55 | | (Nagy et al. 1999) |
| Heart mass | kg | Mammals | 99 | | (Crile and Quiring 1940) |
| Kidney mass | | | 90 | | |
| Liver mass | | | 93 | | |
| Lung mass | | | 93 | | |
| Gastrointestinal tract tissue mass | | | 37 | | |
| Brain mass | | | 450 | using the respective older dataset if species occurred repeatedly in the total collection; correcting rodent data from Mace et al. (1981) by subtracting 0.59 g as described by Isler and van Schaik (2006) | (Crile and Quiring 1940, Sacher and Staffeldt 1974, Mace et al. 1981, McNab and Eisenberg 1989, Savage and West 2007) |
| Lung volume | ml | Mammals | 33 | | (Gehr et al. 1981) |
| Lung alveolar surface area | $m^2$ | | 33 | | |
| Breathing frequency | $min^{-1}$ | Mammals | 56 | excluding bovids as suggested by the authors | (Mortolaa and Lanthier 2005) |
| Heart rate | | | 25 | | (Noujaim et al. 2004) |
| Offspring mass | kg $female^{-1}$ $yr^{-1}$ | Mammals | 521 | | (Jones et al. 2009) |
| Population growth rate ($r_{max}$) | $yr^{-1}$ | Mammals | 291 | note that this dataset has been critized recently by Fagan et al. (2010); note, however, that the shape of scaling in the data compilations of these authors (Fig. 2a and c of their paper) indicates a similar quadratic scaling | (Duncan et al. 2007) |

534

534 Table 2. Comparison of linear (L) and quadratic (Q) regressions of basal (BMR) and field (FMR) metabolic rate in birds and reptiles.

| | *n* | *a* | 95% CI | *b* or $b_1$ | 95% CI | $b_2$ | 95% CI | $AIC_c$ | $\Delta AIC_c$ |
|---|---|---|---|---|---|---|---|---|---|
| ***BMR*** | | | | | | | | | |
| *Birds* | | | | | | | | | |
| Linear ($a+b_1M$) | 530 | 2.4962 | 2.4778, 2.5147 | 0.6508 | 0.6370, 0.6647 | | | -2235.01 | 3.70 |
| Quadratic ($a+b_1M+b_2M^2$) | 530 | 2.4983 | 2.4799, 2.5168 | 0.6821 | 0.6530, 0.7112 | 0.0183 | 0.0033, 0.0333 | -2238.71 | **0.00** |
| *Reptiles* | | | | | | | | | |
| Linear ($a+b_1M$) | 55 | 0.9029 | 0.8090, 0.9969 | 0.8010 | 0.7607, 0.8413 | | | - | - |
| Quadratic ($a+b_1M+b_2M^2$) | 55 | 0.8415 | 0.7116, 0.9713 | 0.7163 | 0.5855, 0.8471 | -0.0220 | -0.0542, 0.0103 | - | - |
| ***FMR*** | | | | | | | | | |
| *Birds* | | | | | | | | | |
| Linear ($a+b_1M$) | 130 | 3.0091 | 2.9635, 3.0547 | 0.6582 | 0.6243, 0.6922 | | | - | - |
| Quadratic ($a+b_1M+b_2M^2$) | 130 | 3.0029 | 2.9536, 3.0523 | 0.6719 | 0.6181, 0.7257 | 0.0109 | -0.0222, 0.0439 | - | - |
| *Reptiles* | | | | | | | | | |
| Linear ($a+b_1M$) | 55 | 1.9571 | 1.8597, 2.0544 | 0.8879 | 0.8289, 0.9469 | | | - | - |
| Quadratic ($a+b_1M+b_2M^2$) | 55 | 1.9441 | 1.8432, 2.0450 | 0.9320 | 0.8249, 1.0391 | 0.0254 | -0.0261, 0.0768 | - | - |

535 $AIC_c$ are only presented when both linear and quadratic model are significant
536

Table 3. Comparison of various models relating body mass (M, kg) to basal metabolic rate (kJ $d^{-1}$) in mammals (n=615) for raw data and under PGLS analyses. Best supported models are highlighted by grey shading.

| Model | | $a$ | 95% CI | $b$ or $b_1$ | 95% CI | $b_2$ | 95% CI | $b_3$ | 95% CI | $AIC_c$ | $\Delta AIC_c$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Raw data*** | | | | | | | | | | | |
| Linear ($a+b_1M$) | | 2.3839 | 2.3685, 2.3992 | | 0.7188 | 0.7069, 0.7307 | | | | -2217.18 | 59.44 |
| Quadratic ($a+b_1M+b_2M^2$) | | 2.3401 | 2.3211, 2.3590 | | 0.7326 | 0.7205, 0.7446 | 0.0320 | 0.0233, 0.0406 | | -2265.79 | 10.83 |
| Composite ($a_e+a_m+b_1M$) | m | 2.2856 | 2.2465, 2.3246 | | 0.7214 | 0.7097, 0.7331 | | | | -2243.34 | 33.27 |
| | e | 2.3979 | 2.3820, 2.4137 | | | | | | | | |
| Composite ($a_e+a_m+b_eM+b_mM$) | m | 2.2871 | 2.2444, 2.3298 | m | 0.7250 | 0.6831, 0.7670 | | | | -2241.36 | 35.26 |
| | e | 2.3976 | 2.3815, 2.4137 | e | 0.7211 | 0.7089, 0.7333 | | | | | |
| Composite ($a_e+a_m+b_{e,L1}M+b_{e,L>1}M+b_mM$) | m | 2.2871 | 2.2457, 2.3286 | m | 0.7250 | 0.6843, 0.7658 | | | | -2276.62 | **0.00** |
| | e | 2.3863 | 2.3703, 2.4023 | eL=1 | 0.7596 | 0.7426, 0.7767 | | | | | |
| | | | | eL>1 | 0.6925 | 0.6776, 0.7074 | | | | | |
| Composite ($a_{e,L1}+a_{e,L>1}+a_m+b_{e,L1}M+b_{e,L>1}M+b_mM$) | m | 2.2871 | 2.2456, 2.3286 | m | 0.7250 | 0.6843, 0.7658 | | | | -2274.58 | **2.04** |
| | eL=1 | 2.3861 | 2.3602, 2.4121 | eL=1 | 0.7596 | 0.7420, 0.7772 | | | | | |
| | eL>1 | 2.3864 | 2.3660, 2.4068 | eL>1 | 0.6925 | 0.6762, 0.7088 | | | | | |
| Composite ($a+b_{e,L1}M+b_{e,L>1}M$) | | 2.3743 | 2.3587, 2.3898 | eL=1 | 0.7533 | 0.7361, 0.7706 | | | | -2238.91 | 37.70 |
| | | | | eL>1 | 0.6948 | 0.6801, 0.7096 | | | | | |
| ***PGLS*** | | | | | | | | | | | |
| Linear ($a+b_1M$) | | 2.2480 | 2.0526, 2.4434 | | 0.7312 | 0.7136, 0.7488 | | | | -819.04 | 7.20 |
| Quadratic ($a+b_1M+b_2M^2$) | | 2.2359 | 2.0452, 2.4266 | | 0.7375 | 0.7197, 0.7553 | 0.0140 | 0.0050, 0.0230 | | -826.24 | **0.00** |
| Linear with interaction ($a+b_1M+ b_2R+ b_3(M*R)$) | | 2.3822 | 2.0983, 2.4629 | | 0.6557 | 0.6618, 0.7265 | -0.0044 | -0.0093, 0.0314 | 0.0193 | 0.0049, 0.0337 | -824.46 | **1.78** |

e eutherians, m marsupials, L=1 with ≤ 1.5 and L>1 with > 1.5 offspring per year, R reproductive type (m, eL1, eL2)

Parameters $a$, $b_1$, $b_2$ correspond with function (2) and function (5), respectively, of the main text

Table 4. Comparison of various models relating body mass (M, kg) to field metabolic rate in mammals (n=120) for raw data and under PGLS analyses. Best supported models are highlighted by grey shading.

| Model | | *a* | 95% CI | *b* or $b_1$ | 95% CI | $b_2$ | 95% CI | $b_3$ | 95% CI | $AIC_c$ | $\Delta AIC_c$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Raw data*** | | | | | | | | | | | |
| Linear ($a+b_1M$) | | 2.8220 | 2.7817, 2.8624 | | 0.6698 | 0.6382, 0.7014 | | | | -383.62 | 16.17 |
| Quadratic ($a+b_1M+b_2M^2$) | | 2.7456 | 2.6920, 2.7991 | | 0.6976 | 0.6649, 0.7304 | 0.0564 | 0.0286, 0.0843 | | -396.98 | **2.81** |
| Composite ($a_e+a_m+b_1M$) | m | 2.7441 | 2.6811, 2.8070 | | 0.6860 | 0.6538, 0.7182 | | | | -391.10 | 8.69 |
| | e | 2.8699 | 2.9205, 2.9193 | | | | | | | | |
| Composite ($a_e+a_m+b_eM+b_mM$) | m | 2.7428 | 2.6824, 2.8033 | m | 0.5927 | 0.5289, 0.6565 | | | | -399.79 | **0.00** |
| | e | 2.8929 | 2.8435, 2.9423 | e | 0.7146 | 0.6793, 0.7499 | | | | | |
| Composite | | | | m | 0.5927 | 0.5291, 0.6563 | | | | | |
| ($a_e+a_m+b_{e,L1}M+b_{e,L>1}M+b_mM$) | m | 2.7428 | 2.6825, 2.8031 | eL=1 | 0.6957 | 0.6503, 0.7411 | | | | -399.38 | **0.41** |
| | e | 2.9002 | 2.8497, 2.9506 | eL>1 | 0.7348 | 0.6881, 0.7815 | | | | | |
| Composite | | | | | | | | | | | |
| ($a_{e,L1}+a_{e,L>1}+a_m+b_{e,L1}M+b_{e,L>1}M+b_mM$) | m | 2.7428 | 2.6824, 2.8033 | m | 0.5927 | 0.5289, 0.6565 | | | | | |
| | eL=1 | 2.9193 | 2.8345, 3.0040 | eL=1 | 0.7008 | 0.6518, 0.7499 | | | | -397.49 | **2.30** |
| | eL>1 | 2.8896 | 2.8265, 2.9527 | eL>1 | 0.7293 | 0.6784, 0.7801 | | | | | |
| Composite ($a+b_{e,L1}M+b_{e,L>1}M$) | | 2.8291 | 2.7864, 2.8718 | eL=1 | 0.6551 | 0.6122, 0.6979 | | | | -382.56 | 17.23 |
| | | | | eL>1 | 0.6859 | 0.6413, 0.7306 | | | | | |
| ***PGLS*** | | | | | | | | | | | |
| Linear ($a+b_1M$) | | 2.7604 | 2.4982, 3.0226 | | 0.6966 | 0.6539, 0.7393 | | | | -68.61 | 3.59 |
| Quadratic ($a+b_1M+b_2M^2$) | | 2.7199 | 2.4651, 2.9747 | | 0.7119 | 0.6680, 0.7558 | 0.0396 | 0.0069, 0.0723 | | -72.20 | **0.00** |
| Linear with interaction ($a+b_1M+ b_2R+ b_3(M*R)$) | | 2.8807 | 2.6032, 3.1582 | | 0.6848 | 0.5895, 0.7801 | -0.0423 | -0.1157, 0.0311 | 0.0073 | -0.0331, 0.0476 | -66.24 | 5.96 |

e eutherians, m marsupials, L=1 with ≤ 1.5 and L>1 with > 1.5 offspring per year, R reproductive type (m, eL1, eL2)

Parameters $a$, $b_1$, $b_2$ correspond with function (2) and function (5), respectively, of the main text

Table 5. Comparison of various models relating body mass (M, kg) to brain mass (kg) in mammals (n=450) for raw data and under PGLS analyses. Best supported models are highlighted by grey shading.

| Model | | *a* | 95% CI | *b* or $b_1$ | 95% CI | $b_2$ | 95% CI | $b_3$ | 95% CI | $AIC_c$ | $\Delta AIC_c$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Raw data*** | | | | | | | | | | | |
| Linear ($a+b_1M$) | | -2.0388 | -2.0580, -2.0195 | | 0.7299 | 0.7158, 0.7440 | | | | -1434.66 | 38.63 |
| Quadratic ($a+b_1M+b_2M^2$) | | -2.0192 | -2.0455, -1.9929 | | 0.7344 | 0.7198, 0.7490 | -0.0097 | -0.0187, -0.0008 | | -1437.18 | 36.10 |
| Composite ($a_e+a_m+b_1M$) | m | -2.1796 | -2.2727, -2.0865 | | 0.7301 | 0.7161, 0.7441 | | | | -1441.82 | 31.47 |
| | e | -2.0328 | -2.0523, -2.0134 | | | | | | | | |
| Composite ($a_e+a_m+b_eM+b_mM$) | m | -2.1716 | -2.2718, -2.0713 | m | 0.7633 | 0.6098, 0.9168 | | | | -1439.98 | 33.30 |
| | e | -2.0329 | -2.0524, -2.0134 | e | 0.7298 | 0.7158, 0.7439 | | | | | |
| Composite | m | -2.1716 | -2.2719, -2.0712 | m | 0.7633 | 0.6097, 0.9170 | | | | -1438.01 | 35.27 |
| ($a_e+a_m+b_{e,L1}M+b_{e,L>1}M+b_mM$) | e | -2.0346 | -2.0572, -2.0120 | eL=1 | 0.7322 | 0.7112, 0.7531 | | | | | |
| | | | | eL>1 | 0.7274 | 0.7058, 0.7489 | | | | | |
| Composite | m | -2.1716 | -2.2679, -2.0752 | m | 0.7633 | 0.6157, 0.9109 | | | | -1473.28 | **0.00** |
| ($a_{e,L1}+a_{e,L>1}+a_m+b_{e,L1}M+b_{e,L>1}M+b_mM$) | eL=1 | -1.9443 | -1.9802, -1.9083 | eL=1 | 0.7117 | 0.6906, 0.7328 | | | | | |
| | eL>1 | -2.0864 | -2.1136, -2.0592 | eL>1 | 0.7023 | 0.6802, 0.7245 | | | | | |
| Composite ($a+b_{e,L1}M+b_{e,L>1}M$) | | -2.0411 | -2.0634, -2.0189 | eL=1 | 0.7332 | 0.7121, 0.7543 | | | | -1432.81 | 40.48 |
| | | | | eL>1 | 0.7264 | 0.7049, 0.7480 | | | | | |
| ***PGLS*** | | | | | | | | | | | |
| Linear ($a+b_1M$) | | -2.1066 | -2.3704, -1.8428 | | 0.6330 | 0.6105, 0.6555 | | | | -464.14 | 10.10 |
| Quadratic ($a+b_1M+b_2M^2$) | | -2.0937 | -2.3581, -1.8293 | | 0.6360 | 0.6133, 0.6587 | -0.0108 | -0.0202, -0.0014 | | -467.21 | 7.03 |
| Linear with interaction ($a+b_1M+ b_2R+ b_3(M*R)$) | | -2.1834 | -2.4346, -1.9321 | | 0.5675 | 0.5260, 0.6089 | 0.0283 | -0.0003, 0.0568 | 0.0316 | 0.0138, 0.0495 | -474.24 | **0.00** |

e eutherians, m marsupials, L=1 with ≤ 1.5 and L>1 with > 1.5 offspring per year, R reproductive type (m, eL1, eL2)

Parameters $a$, $b_1$, $b_2$ correspond with function (2) and function (5), respectively, of the main text

549 Table 6. Comparison of various models relating body mass (M, kg) to offspring mass (kg female$^{-1}$ year$^{-1}$) mass in mammals (n=521) for raw data
550 and under PGLS analyses. Best supported models are highlighted by grey shading.

| Model | | $a$ | 95% CI | $b$ or $b_1$ | | 95% CI | $b_2$ | 95% CI | $b_3$ | 95% CI | $AIC_c$ | $\Delta AIC_c$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Raw data*** | | | | | | | | | | | | |
| Linear ($a+b_1M$) | | 1.9977 | 1.9240, 2.0714 | | 0.6899 | 0.6406, 0.7392 | | | | | -255.55 | 838.07 |
| Quadratic ($a+b_1M+b_2M^2$) | | 1.9110 | 1.8142, 2.0079 | | 0.6711 | 0.6202, 0.7220 | 0.0336 | 0.0090, 0.0581 | | | -260.74 | 832.88 |
| Composite ($a_e+a_m+b_1M$) | m | -0.2060 | -0.3283, -0.0838 | | 0.7224 | 0.6967, 0.7482 | | | | | -933.42 | 160.20 |
| | e | 2.2177 | 2.1775, 2.2578 | | | | | | | | | |
| Composite ($a_e+a_m+b_eM+b_mM$) | m | -0.3488 | -0.4679, -0.2297 | m | 0.2625 | 0.1542, 0.3708 | | | | | -1000.41 | 93.21 |
| | e | 2.2330 | 2.1953, 2.2708 | e | 0.7464 | 0.7217, 0.7712 | | | | | | |
| Composite | m | -0.3488 | -0.4603, -0.2372 | m | 0.2625 | 0.1611, 0.3640 | | | | | -1067.40 | 26.22 |
| ($a_e+a_m+b_{e,L1}M+b_{e,L>1}M+b_mM$) | e | 2.1793 | 2.1418, 2.2168 | eL=1 | 0.8127 | 0.7850, 0.8404 | | | | | | |
| | | | | eL>1 | 0.6157 | 0.5777, 0.6536 | | | | | | |
| Composite | m | -0.3488 | -0.4575, -0.2401 | m | 0.2625 | 0.1637, 0.3614 | | | | | -1093.62 | **0.00** |
| ($a_{e,L1}+a_{e,L>1}+a_m+b_{e,L1}M+b_{e,L>1}M+b_mM$) | eL=1 | 2.0783 | 2.0263, 2.1303 | eL=1 | 0.8015 | 0.7742, 0.8288 | | | | | | |
| | eL>1 | 2.2774 | 2.2261, 2.3286 | eL>1 | 0.6656 | 0.6244, 0.7069 | | | | | | |
| Composite ($a+b_{e,L1}M+b_{e,L>1}M$) | | 1.9574 | 1.8795, 2.0352 | eL=1 | 0.7409 | 0.6815, 0.8003 | | | | | -262.31 | 831.31 |
| | | | | eL>1 | 0.5960 | 0.5169, 0.6751 | | | | | | |
| ***PGLS*** | | | | | | | | | | | | |
| Linear ($a+b_1M$) | | 2.0814 | 1.5873, 2.5755 | | 0.7219 | 0.6825, 0.7613 | | | | | 148.47 | 4.49 |
| Quadratic ($a+b_1M+b_2M^2$) | | 2.0751 | 1.5814, 2.5688 | | 0.7219 | 0.6825, 0.7613 | 0.0046 | -0.0111, 0.0203 | | | 149.60 | 5.62 |
| Linear with interaction ($a+b_1M+ b_2R+ b_3(M*R)$) | | -1.510 | -2.1291, -1.0330 | | 0.5806 | 0.5026, 0.6587 | -0.0364 | -0.0992, 0.0264 | 0.0340 | 0.0014, 0.0667 | 143.99 | **0.00** |

551 e eutherians, m marsupials, L=1 with ≤ 1.5 and L>1 with > 1.5 offspring per year, R reproductive type (m, eL1, eL2)
552 Parameters $a$, $b_1$, $b_2$ correspond with function (2) and function (5), respectively, of the main text
553

554 Table 7. Comparison of linear various models relating body mass (M, kg) to population growth rate ($r_{max}$) in mammals (n=291) for raw data and
555 under PGLS analysis. Best supported models are highlighted by grey shading.

| Model | | *a* | 95% CI | *b* or $b_1$ | | 95% CI | $b_2$ | 95% CI | $b_3$ | 95% CI | $AIC_c$ | $\Delta AIC_c$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Raw data*** | | | | | | | | | | | | |
| Linear ($a+b_1M$) | | -0.1784 | -0.2208, -0.1360 | | -0.2620 | -0.2885, -0.2356 | | | | | -634.08 | 129.49 |
| Quadratic ($a+b_1M+b_2M^2$) | | -0.2109 | -0.2559, -0.1660 | | -0.3041 | -0.3382, -0.2699 | 0.0234 | 0.0110, 0.0358 | | | -645.62 | 117.96 |
| Composite ($a_e+a_m+b_1M$) | m | -0.0428 | -0.1111, 0.0255 | | -0.2312 | -0.2596, -0.2029 | | | | | -655.09 | 108.49 |
| | e | -0.2662 | -0.3203, -0.2121 | | | | | | | | | |
| Composite ($a_e+a_m+b_eM+b_mM$) | m | -0.0391 | -0.1098, 0.0317 | m | -0.2196 | -0.2829, -0.1562 | | | | | -653.20 | 110.38 |
| | e | -0.2631 | -0.3194, -0.2067 | e | -0.2342 | -0.2659, -0.2024 | | | | | | |
| Composite | m | -0.0391 | -0.1098, 0.0316 | m | -0.2196 | -0.2829, -0.1562 | | | | | -652.31 | 111.27 |
| ($a_e+a_m+b_{e,L1}M+b_{e,L>1}M+b_mM$) | e | -0.2700 | -0.3277, -0.2123 | eL=1 | -0.2266 | -0.2612, -0.1920 | | | | | | |
| | | | | eL>1 | -0.2701 | -0.3429, -0.1972 | | | | | | |
| Composite | m | -0.0391 | -0.0974, 0.0192 | m | -0.2196 | -0.2718, -0.1673 | | | | | -763.57 | **0.00** |
| ($a_{e,L1}+a_{e,L>1}+a_m+b_{e,L1}M+b_{e,L>1}M+b_mM$) | eL=1 | -0.5460 | -0.6127, -0.4794 | eL=1 | -0.1219 | -0.1554, -0.0883 | | | | | | |
| | eL>1 | 0.0173 | -0.0507, 0.0853 | eL>1 | -0.2925 | -0.3527, -0.2324 | | | | | | |
| Composite ($a+b_{e,L1}M+b_{e,L>1}M$) | | -0.1879 | -0.2369, -0.1390 | eL=1 | -0.2539 | -0.2876, -0.2202 | | | | | -632.64 | 130.94 |
| | | | | eL>1 | -0.2803 | -0.3341, -0.2266 | | | | | | |
| ***PGLS*** | | | | | | | | | | | | |
| Linear ($a+b_1M$) | | -0.1167 | -0.5142, 0.2808 | | -0.2149 | -0.2547, -0.1751 | | | | | -89.23 | 34.59 |
| Quadratic ($a+b_1M+b_2M^2$) | | -0.1277 | -0.5230, 0.2676 | | -0.2282 | -0.2735, -0.1829 | 0.0089 | -0.0060, 0.0238 | | | -88.59 | 35.23 |
| Linear with interaction ($a+b_1M+ b_2R+ b_3(M*R)$) | | 0.2627 | -0.0773, 0.6027 | | -0.3249 | -0.4103, -0.2396 | -0.1724 | -0.2246, -0.1202 | 0.0581 | 0.0238, 0.0923 | -123.82 | **0.00** |

556 e eutherians, m marsupials, L=1 with ≤ 1.5 and L>1 with > 1.5 offspring per year, R reproductive type (m, eL1, eL2)
557 Parameters $a$, $b_1$, $b_2$ correspond with function (2) and function (5), respectively, of the main text
558

559 **Online supplement**
560

561 **Table S1.** Sensitivity of linear (L) and quadratic (Q) scaling to sample size, from regressions
562 fitted to 3 x $10^4$ random subsamples derived from the mammal and bird basal MR datasets.

| Total *n* | % of dataset extracted | *n* per subsample | Model | Mean $R^2$ | Mean AIC | *p* (*a*) | *p* (*b* or $b_1$) | *p* ($b_2$) | *p* (best-fit) |
|---|---|---|---|---|---|---|---|---|---|
| **Mammals** | | | | | | | | | |
| 637 | 10 | 64 | L | 0.9576 | -112.310 | <0.0001 | <0.0001 | | 0.4988 |
| | | | Q | 0.9601 | -112.851 | <0.0001 | <0.0001 | 0.4218 | 0.5012 |
| | 25 | 159 | L | 0.9577 | -285.089 | <0.0001 | <0.0001 | | 0.6077 |
| | | | Q | 0.9606 | -287.871 | <0.0001 | <0.0001 | 0.0650 | 0.3923 |
| | 50 | 319 | L | 0.9578 | -569.115 | <0.0001 | <0.0001 | | 0.9994 |
| | | | Q | 0.9608 | -579.596 | <0.0001 | <0.0001 | 0.0002 | 0.0006 |
| | 75 | 478 | L | 0.9578 | -854.634 | <0.0001 | <0.0001 | | |
| | | | Q | 0.9609 | -871.320 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| **Birds** | | | | | | | | | |
| 530 | 10 | 53 | L | 0.9405 | -109.481 | <0.0001 | <0.0001 | | 0.0952 |
| | | | Q | 0.9403 | -107.878 | <0.0001 | <0.0001 | 0.8585 | 0.9048 |
| | 25 | 133 | L | 0.9411 | -277.165 | <0.0001 | <0.0001 | | 0.1718 |
| | | | Q | 0.9414 | -275.973 | <0.0001 | <0.0001 | 0.7579 | 0.8282 |
| | 50 | 265 | L | 0.9413 | -556.608 | <0.0001 | <0.0001 | | 0.2674 |
| | | | Q | 0.9417 | -555.990 | <0.0001 | <0.0001 | 0.6258 | 0.7326 |
| | 75 | 398 | L | 0.9414 | -836.061 | <0.0001 | <0.0001 | | 0.3749 |
| | | | Q | 0.9418 | -835.938 | <0.0001 | <0.0001 | 0.4183 | 0.6251 |

This table shows that a linear allometric fit and its parameters remain significant irrespective of the size and M range of the sample, but the parameter $b_2$ of a quadratic fit becomes less significant at smaller sample sizes. Accordingly, in smaller datasets, the relative strength of quadratic over linear models is likely to be lost, even in cases where $b_2$ retains its significance.

Birds are an extreme example: in the whole dataset, a quadratic function provides a slightly better fit compared with a linear function, but this preference rapidly subsides, as does the significance of the polynomial term, in smaller data subsets.

These results suggest that sample size may influence statistical power, particularly of quadratic regressions, when comparing linear with non-linear scaling in allometry. We demonstrate below that these effects of sample size are, however, not entirely an effect of reduced statistical power, but are more likely influenced by the range of M included in a dataset.

563

563 The figures below show the influence of body mass (M) distributions on linear and quadratic
564 fits. M distributions were manipulated in the mammal (Part 1) and bird (Part 2) basal MR
565 datasets by random resampling. We explore the effect of M range and mean M, and of the
566 minimum and maximum M point included in a dataset, on three statistics related to a
567 comparison of linear (L) with quadratic (Q) scaling: significance of the allometric exponent
568 ($b$), significance of the polynomial term ($b_2$), and the evidence to support a better fit of Q to L
569 (lower AIC score for Q). The mean ± 1 standard error for each of these statistics, derived
570 from 3 x $10^4$ permutations, are shown.
571
572 In both datasets, the parameters $a$, $b$ and $b_1$ for the respective equations were consistently
573 significant, but the polynomial term $b_2$ was not. In mammals, a linear increase of $b_1$ with M
574 on a logarithmic scale is evident (Fig. S1.2a), and is a condition supporting that any curvature
575 in allometry solves to a quadratic polynomial (equations 3-5 in the main text). However,
576 significance of the polynomial term is only evident when the M range is at least 4, possibly 5,
577 orders of magnitude (Fig. S1.1b), and this condition may be missing in smaller datasets.
578 Similarly, whereas the polynomial term and quadratic fit is unanimously favored for mammal
579 BMR in larger datasets, this support is reduced in smaller datasets, for example if the data do
580 not include species below log(M) ≈ -2.0 (i.e. 0.01 kg, or 10 g; Fig. S1.3a), or excludes species
581 above log(M) ≈ 3.0 (i.e. 1000 kg; Fig. S1.4a). In summary, larger datasets are likely to
582 include a wide range of M, from where quadratic scaling would be evident, but in datasets
583 excluding species < 0.01 kg and/or > 1000 kg, quadratic scaling is unlikely to be detected.
584 This indicates that quadratic scaling is an artefact of changes in allometry at the extreme ends
585 of the M range. For birds, similar rules for the detection of quadratic scaling could be found:
586 simply, scaling appears to be linear except in the entire dataset, strongly indicating a spurious
587 result for the significance of a quadratic fit.
588

**Supplementary figures Part 1: Mammal BMR**

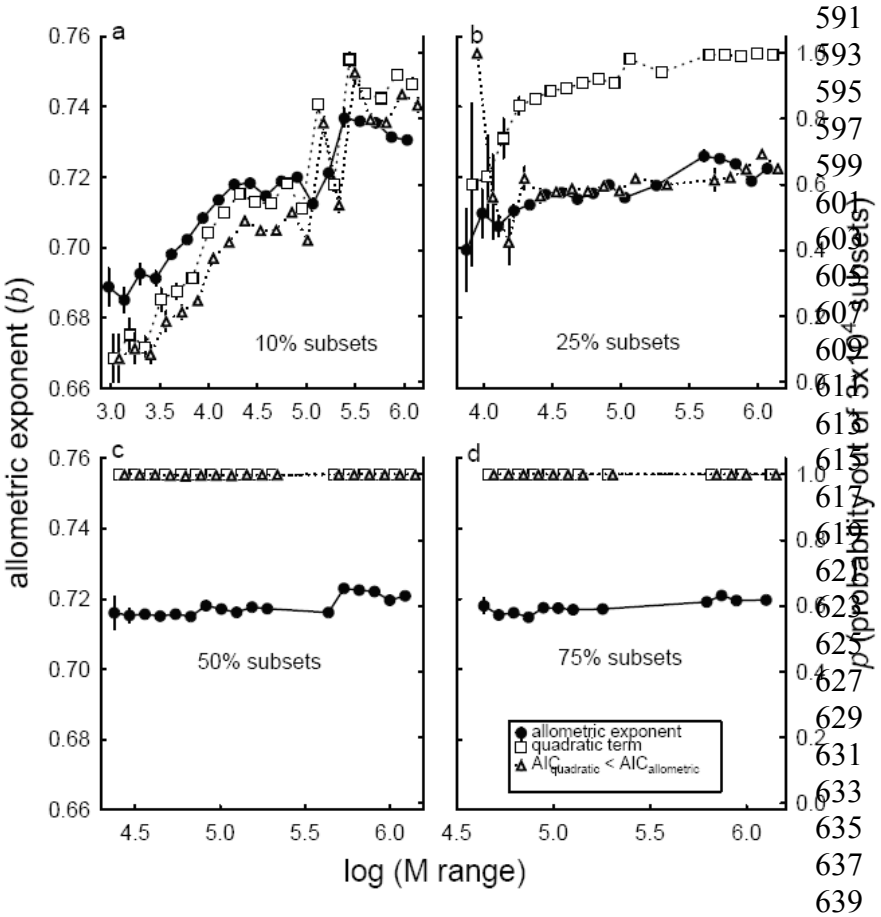



**Fig. S1.1.** Response of i) the simple allometric exponent *b* (solid circles); ii) probability of a significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic function provides a better-fit to log-transformed data than the linear function (probability of lower AIC score in the former) (open triangles), to increases in the range of body mass (M, kg) included in the data (maximum – minimum M). M ranges were manipulated by random subsamples representing 10 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with $3x10^4$ permutations.

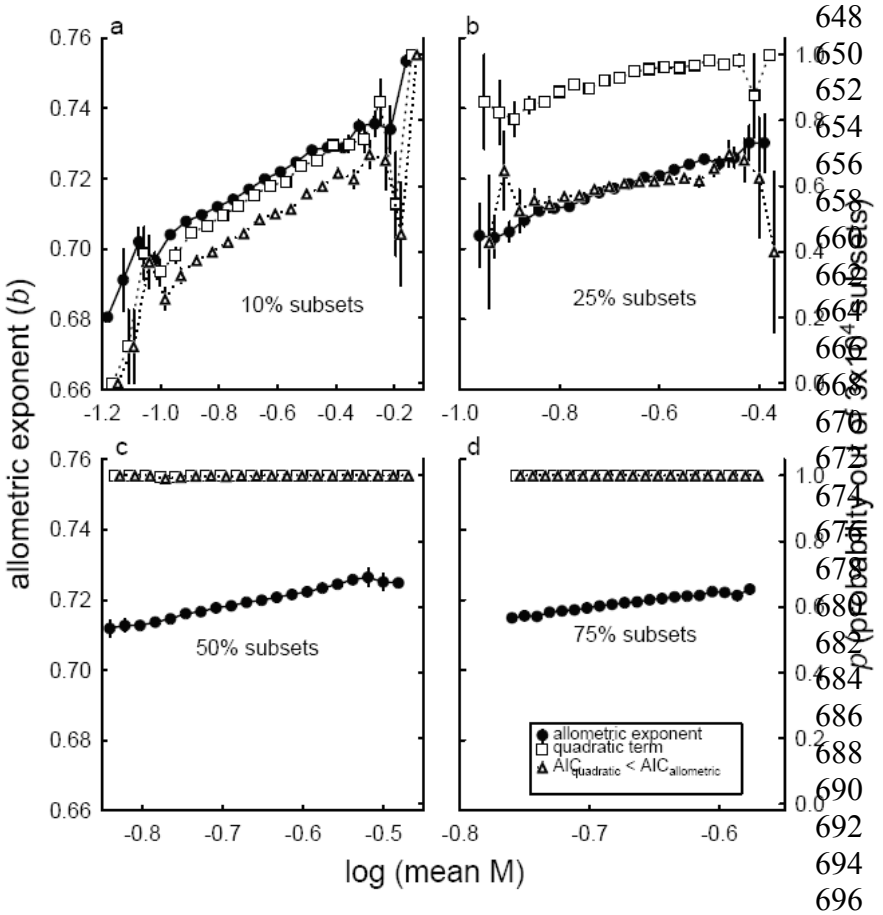



**Fig. S1.2.** Response of i) the simple allometric exponent *b* (solid circles); ii) probability of a significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic function provides a better-fit to log-transformed data than the linear function (probability of lower AIC score in the former) (open triangles), to increases in the mean body mass (M, kg) included in the data. M ranges were manipulated by random subsamples representing 10 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with $3x10^4$ permutations.

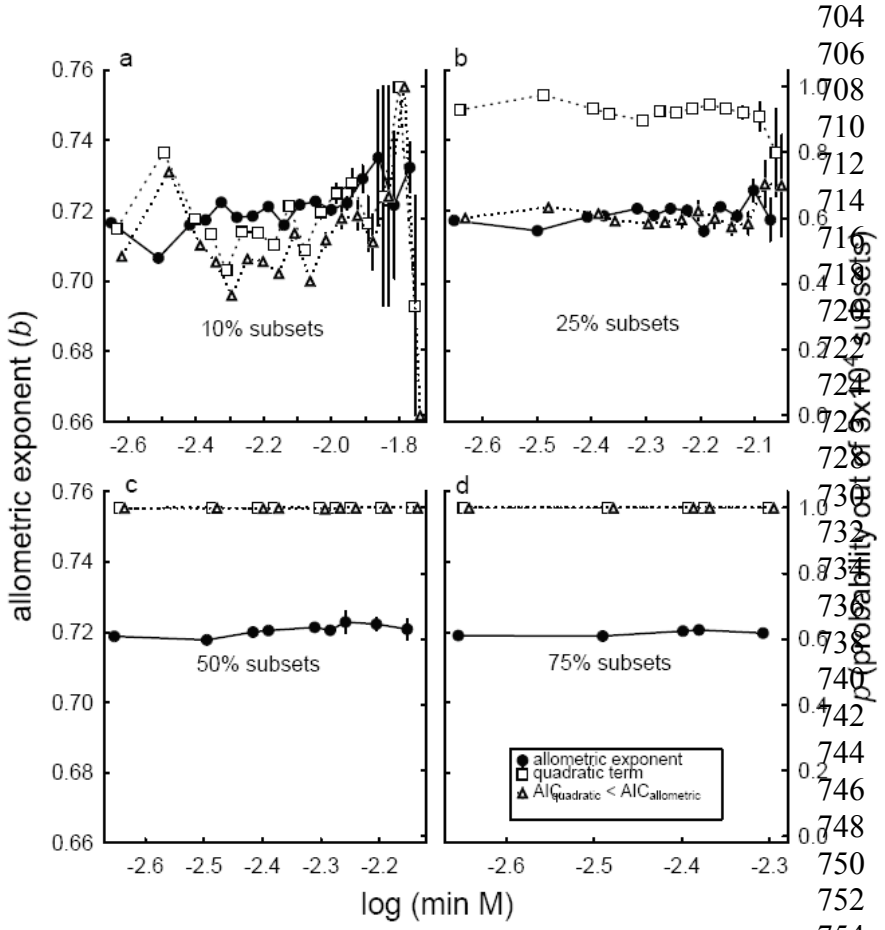



**Fig. S1.3.** Response of i) the simple allometric exponent *b* (solid circles); ii) probability of a significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic function provides a better-fit to log-transformed data than the linear function (probability of lower AIC score in the former) (open triangles), to increases in the minimum body mass (M, kg) included in the data. M ranges were manipulated by random subsamples representing 10 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with $3x10^4$ permutations.

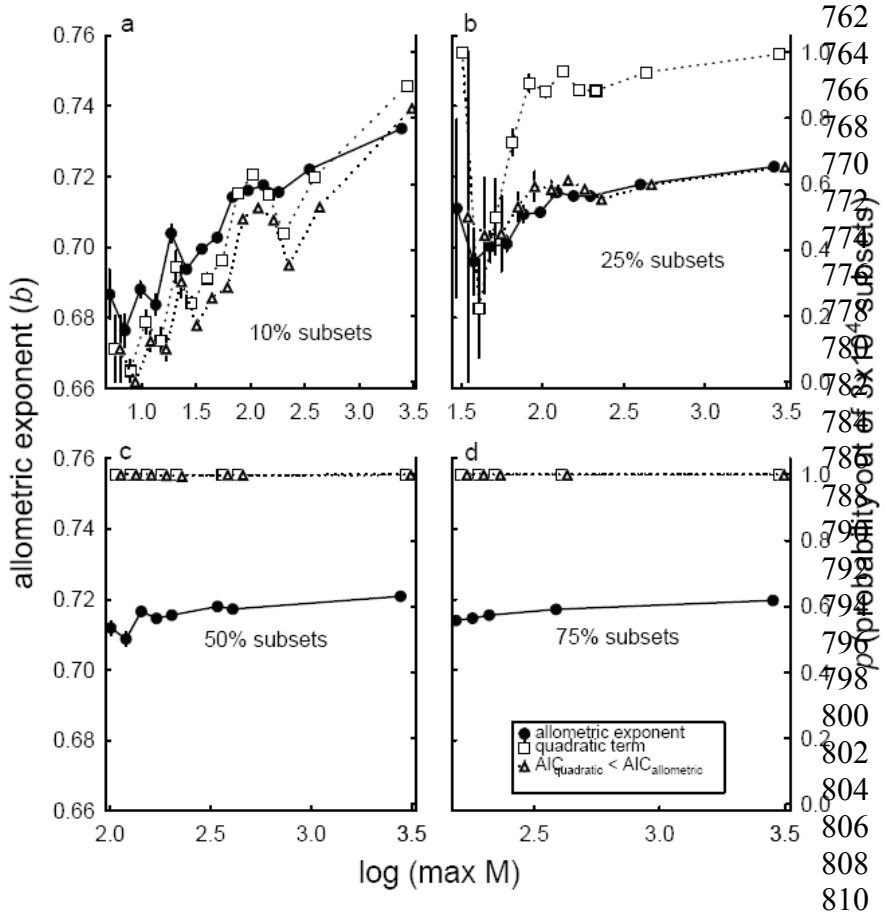



**Fig. S1.4.** Response of i) the simple allometric exponent *b* (solid circles); ii) probability of a significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic function provides a better-fit to log-transformed data than the linear function (probability of lower AIC score in the former) (open triangles), to increases in the maximum body mass (M, kg) included in the data. M ranges were manipulated by random subsamples representing 10 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with $3x10^4$ permutations.

**Supplementary figures Part 2: Bird BMR**

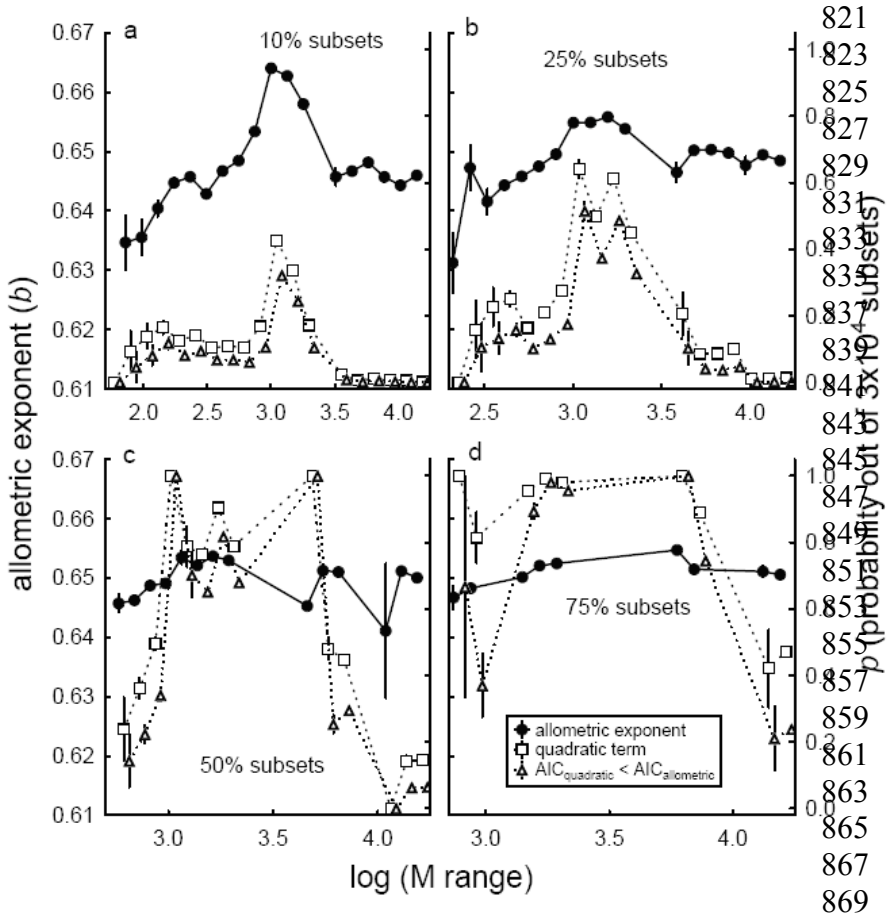



**Fig. S2.1.** Response of i) the simple allometric exponent *b* (solid circles); ii) probability of a significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic function provides a better-fit to log-transformed data than the linear function (probability of lower AIC score in the former) (open triangles), to increases in the range of body mass (M, kg) included in the data (maximum – minimum M). M ranges were manipulated by random subsamples representing 10 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with $3x10^4$ permutations.

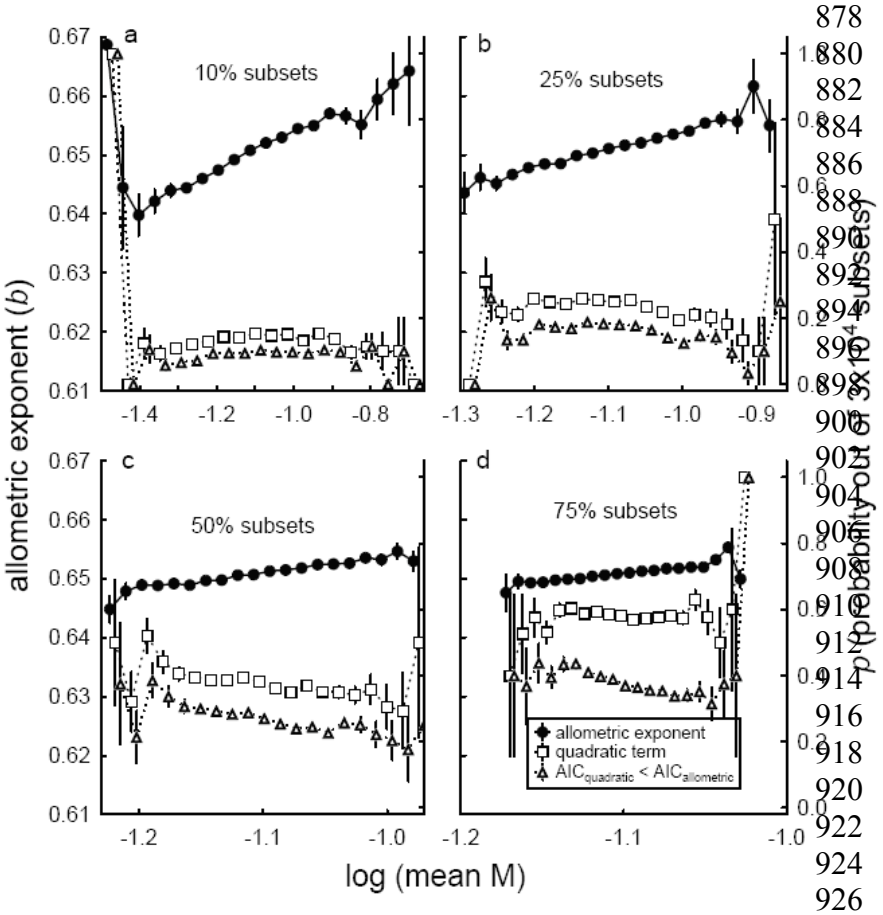
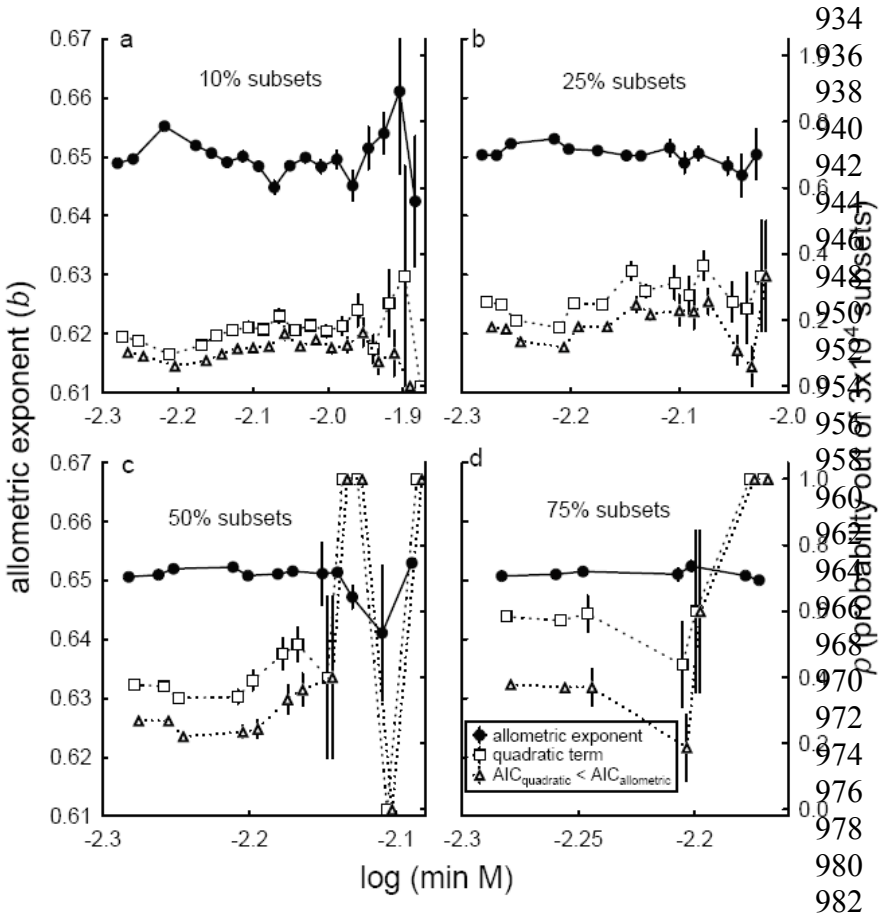



**Fig. S2.2.** Response of i) the simple allometric exponent *b* (solid circles); ii) probability of a significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic function provides a better-fit to log-transformed data than the linear function (probability of lower AIC score in the former) (open triangles), to increases in the mean body mass (M, kg) included in the data. M ranges were manipulated by random subsamples representing 10 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with $3x10^4$ permutations.




983 **Fig. S2.3.** Response of i) the simple allometric exponent *b* (solid circles); ii) probability of a
984 significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic
985 function provides a better-fit to log-transformed data than the linear function (probability of
986 lower AIC score in the former) (open triangles), to increases in the minimum body mass (M,
987 kg) included in the data. M ranges were manipulated by random subsamples representing 10
988 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with $3x10^4$ permutations.
989

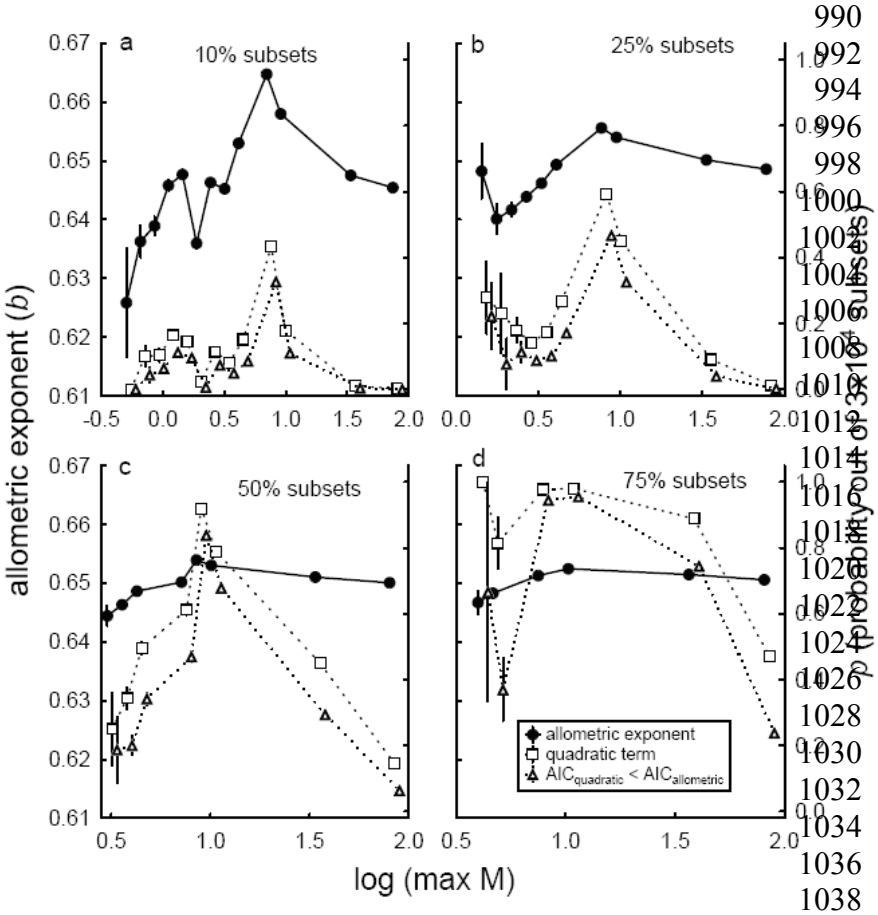



**Fig. S2.4.** Response of i) the simple allometric exponent *b* (solid circles); ii) probability of a significant ($p < 0.05$) quadratic term (open squares); and iii) probability that the quadratic function provides a better-fit to log-transformed data than the linear function (probability of lower AIC score in the former) (open triangles), to increases in the maximum body mass (M, kg) included in the data. M ranges were manipulated by random subsamples representing 10 % (a), 25 % (b), 50 % (c), or 75 % (d) of the data, with $3x10^4$ permutations.

Table S2a. Comparison of linear (L) and quadratic (Q) regressions for raw data of anatomical and physiological traits on body mass (kg) in mammals. All variables were log-transformed prior to analysis. Note that the quadratic term was not significant in any case.

| Trait | Shape | *n* | *a* | -95% CI | +95 % CI | *b* or $b_1$ | -95% CI | +95 % CI | $b_2$ | -95% CI | +95 % CI |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Organ mass** | | | | | | | | | | | |
| Heart | L | 82 | -2.2123 | -2.2575 | -2.1671 | 0.9754 | 0.9454 | 1.0055 | | | |
| | Q | 82 | -2.2175 | -2.2648 | -2.1703 | 0.9624 | 0.9171 | 1.0076 | 0.0076 | -0.0121 | 0.0274 |
| Kidney | L | 74 | -2.1452 | -2.1918 | -2.0987 | 0.8686 | 0.8381 | 0.8990 | | | |
| | Q | 74 | -2.1473 | -2.1969 | -2.0978 | 0.8641 | 0.8182 | 0.9099 | 0.0027 | -0.0175 | 0.0228 |
| Liver | L | 76 | -1.4902 | -1.5306 | -1.4498 | 0.8998 | 0.8733 | 0.9263 | | | |
| | Q | 76 | -1.4889 | -1.5317 | -1.4461 | 0.9026 | 0.8628 | 0.9424 | -0.0017 | -0.0192 | 0.0159 |
| Lung | L | 76 | -1.9663 | -2.0292 | -1.9034 | 1.0141 | 0.9724 | 1.0559 | | | |
| | Q | 76 | -1.9843 | -2.0496 | -1.9189 | 0.9730 | 0.9113 | 1.0347 | 0.0242 | -0.0028 | 0.0511 |
| GIT | L | 32 | -1.0855 | -1.2114 | -0.9596 | 1.0150 | 0.9457 | 1.0843 | | | |
| | Q | 32 | -1.0863 | -1.2201 | -0.9524 | 1.0133 | 0.8986 | 1.1280 | 0.0009 | -0.0439 | 0.0456 |
| **Respiratory and circulation** | | | | | | | | | | | |
| Lung volume | L | 32 | 1.6668 | 1.6195 | 1.7141 | 1.0549 | 1.0273 | 1.0825 | | | |
| | Q | 32 | 1.7025 | 1.6299 | 1.7750 | 1.0587 | 1.0307 | 1.0866 | -0.0125 | -0.0320 | 0.0069 |
| Lung alvolar surface | L | 32 | 0.5363 | 0.4844 | 0.5882 | 0.9358 | 0.9055 | 0.9661 | | | |
| | Q | 32 | 0.4940 | 0.4148 | 0.5732 | 0.9313 | 0.9008 | 0.9618 | 0.0149 | -0.0064 | 0.0362 |
| Breathing frequency | L | 53 | 1.7410 | 1.6614 | 1.8206 | -0.2379 | -0.2793 | -0.1965 | | | |
| | Q | 53 | 1.7326 | 1.6489 | 1.8164 | -0.2560 | -0.3237 | -0.1883 | 0.0091 | -0.0178 | 0.0360 |
| Heart rate | L | 23 | 2.3466 | 2.2945 | 2.3987 | -0.2034 | -0.2305 | -0.1764 | | | |
| | Q | 23 | 2.3513 | 2.2955 | 2.4072 | -0.1944 | -0.2376 | -0.1511 | -0.0041 | -0.0190 | 0.0109 |

Parameters $a$, $b_1$, $b_2$ correspond with function (2) and function (5), respectively, of the main text

Table S2b. Comparison of linear (L) and quadratic (Q) regressions for Phylogenetic Generalized Least-Squares of anatomical and physiological traits on body mass (kg) in mammals. All variables were log-transformed prior to analysis. Note that the quadratic term was not significant in any case.

| Trait | Shape | *a* | -95% CI | +95 % CI | *b* or $b_1$ | -95% CI | +95 % CI | $b_2$ | -95% CI | +95 % CI |
|---|---|---|---|---|---|---|---|---|---|---|
| **Organ mass** | | | | | | | | | | |
| Heart | L | -2.2454 | -2.3881 | -2.1027 | 0.9465 | 0.9120 | 0.9810 | | | |
| | Q | -2.2488 | -2.3921 | -2.1055 | 0.9377 | 0.8854 | 0.9900 | 0.0047 | -0.0159 | 0.0253 |
| Kidney | L | -2.1508 | -2.2941 | -2.0075 | 0.8749 | 0.8414 | 0.9084 | | | |
| | Q | -2.1594 | -2.3021 | -2.0167 | 0.8561 | 0.8055 | 0.9067 | 0.0098 | -0.0102 | 0.0298 |
| Liver | L | -1.4631 | -1.5558 | -1.3704 | 0.8941 | 0.8659 | 0.9223 | | | |
| | Q | -1.4734 | -1.5671 | -1.3797 | 0.8696 | 0.8269 | 0.9123 | 0.0132 | -0.0040 | 0.0304 |
| Lung | L | -1.9589 | -2.0728 | -1.8450 | 1.0024 | 0.9544 | 1.0504 | | | |
| | Q | -1.9625 | -2.0142 | -1.9108 | 0.9764 | 0.9058 | 1.0470 | 0.0215 | -0.0083 | 0.0513 |
| GIT | L | -0.9959 | -1.1400 | -0.8518 | 0.9803 | 0.9070 | 1.0536 | | | |
| | Q | -0.9937 | -1.3396 | -0.6478 | 1.2211 | 1.1719 | 1.2703 | -0.0454 | -0.0932 | 0.0024 |
| **Respiratory and circulation** | | | | | | | | | | |
| Lung volume | L | 1.6513 | 1.5468 | 1.7558 | 1.0114 | 0.9687 | 1.0541 | | | |
| | Q | 1.6691 | 1.5568 | 1.7814 | 1.0188 | 0.9729 | 1.0647 | -0.0080 | -0.0270 | 0.0110 |
| Lung alvolar surface | L | 0.5086 | 0.3761 | 0.6411 | 0.9174 | 0.8666 | 0.9682 | | | |
| | Q | 0.4732 | 0.3291 | 0.6173 | 0.9032 | 0.8495 | 0.9569 | 0.0159 | -0.0049 | 0.0367 |
| Breathing frequency | L | 1.7532 | 1.6658 | 1.8406 | -0.2414 | -0.2845 | -0.1983 | | | |
| | Q | 1.7406 | 1.6783 | 1.8029 | -0.2557 | -0.3116 | -0.1998 | 0.0099 | -0.0146 | 0.0344 |
| Heart rate | L | 2.3541 | 2.2831 | 2.4251 | -0.2087 | -0.2381 | -0.1793 | | | |
| | Q | 2.3671 | 2.3485 | 2.3857 | -0.1834 | -0.2057 | -0.1611 | -0.0083 | -0.0187 | 0.0021 |

Parameters $a$, $b_1$, $b_2$ correspond with function (2) and function (5), respectively, of the main text